Refugia foragers to invasive farmers: socio-environmental transitions during the early Holocene in the Balkans

By Marc Vander Linden

Institute for the Modelling of Socio-Environmental Transitions

Bournemouth University

E-mail: mvanderlinden@bournemouth.ac.uk

Abstract

The early Holocene in the Balkans is synonymous with extensive transformations of both environments and human societies. The new climatic conditions indeed led to a spatial expansion of thermophilous (warmth-loving) plant and animal species that were previously confined to refugial areas, eventually reshaping the local biomes, while glacial species disappeared from the region. These processes were paralleled by profound transformations in the distribution of the foraging populations, the existing yet sparse documentation suggesting clustering in specific ecological niches (e.g. Iron Gates, shores of the Adriatic coast). It is upon this template that, towards the second half of the 9th millennium cal BP, cultigens and animal domesticates appear in the local archaeological record, apparently under the impetus of an incoming population of eventual Near Eastern origins, as suggested by recent ancient DNA ('aDNA') research. This contribution will review the available environmental and archaeological evidence for the early Holocene, focusing on the extent to which ecological factors drove variation in human behaviours, especially food acquisition techniques (either foraging or farming). Particular attention will also be devoted to the identification and characterisation of population history as inferred from multiple categories of evidence, such as the 14C record, settlement patterns, aDNA.

Key-words

Holocene, Mesolithic, Neolithic, demography, human-environment interactions

Biographical note

Marc Vander Linden in a senior lecturer in archaeological modelling at the Institute for the Modelling of Socio-environmental transitions, Bournemouth University. His research interests include human-environment interactions, especially through the lens of early farming regimes, population history, archaeological modelling and the use of legacy data. He has conducted fieldwork in both academic and development-led contexts in various countries, including Belgium, the UK, Syria, Bosnia and Herzegovina and Montenegro.

Introduction

Set in evolutionary terms, the Holocene may not appear at first sight as the most interesting period for archaeology: relatively short when compared to the preceding Pleistocene, it harbours limited biological variety as humankind is restricted to a single species, distributed across all main global landmasses, Antarctica excepted. And yet, as the interglacial climatic conditions lead to extensive reshaping of the landscapes and countless associated human adaptations, this is also the period which sees the regional development and subsequent worldwide dispersal of a variety of plants and animal domesticates, as well as an ever-growing anthropogenic impact upon environments and, eventually, the biosphere. As these complex trajectories unfold upon a multiplicity of temporal and spatial scales, it is often difficult to disentangle the complex inter-relationships linking environments and humans, especially so for older periods where the documentation can be sparse. To what extent past people's behaviour was shaped by or modified local landscapes? How can we identify such patterns using palaeo-records, either environmental or archaeological?

This chapter aims at partially answering these questions for the early Holocene in the Balkans. This choice is justified by several reasons. Firstly, with the onset of the Holocene, the area sees the spatial expansion of thermophilous (warmth-loving) plant and animal species that were previously confined to refugial areas (e.g. Medial & Diadema 2009, Zhelev 2017, Masi *et al*. 2018), eventually reshaping the local biomes as glacial species disappeared from the region. Secondly, towards the second half of the 9th millennium cal BP, cultigens and animal domesticates appear in the local archaeological record, prelude to their further extension across the European peninsula (e.g. Bocquet-Appel *et al*. 2009). Existing archaeological scenarios for these periods disagree on the putative role of demographic forces at play, some stressing continuity across the forager-farmer spectrum, others alternatively insisting upon profound differences between Pleistocene and Holocene foragers, and between Holocene foragers and farmers. Consequently, the present contribution explicitly puts demographic reasoning at the core of the argument, by investigating changes in population size, structure and composition, and how these possibly relate to the ecological niches used by the corresponding past human communities.

The Mesolithic – early Holocene foragers

The Pleistocene – Holocene transition is set by the International Union of Geological Sciences at 11650 calBP (±99 years) on basis of the NGRIP ice core record from Greenland (Walker *et al.* 2009). This global climatic event induces different answers in local environments and, in the Balkans, changes are observed in the spatial extension of numerous plant and animal species otherwise confined to refugia (e.g. Sommer et al. 2008, Medial & Diadema 2009, Stamatis et al. 2009, Meiry *et al*. 2013, Zhelev 2017). Although the precise timing and scale of this process varies from species to species, and keeping in mind the scarcity of available local long-term palaeoenvironmental archives (but see Panagiotopoulos *et al*. 2013, Tonkov *et al*. 2014), overall the early Holocene corresponds in the Balkans to the expanded distribution of deciduous woodlands and a wider availability of potential animal prey (see recent summaries in Pillar Birch and Miracle 2017, Pilaar Birch and Vander Linden 2018). In addition, the Adriatic coastlines also undertook rapid reshaping due to rise in sea-level during the Late Pleistocene and Early Holocene, leading to the flooding of extensive areas in the northern Adriatic and the isolation of several islands along the eastern Adriatic coast (e.g. Surić *et al*. 2005, Surić and Juračić 2010, Dean *et al*. 2020).

The impact of this transformation of both landscapes and seascapes upon human communities is subject to a long and unresolved debate. Whilst numerous elements point to a continuous development of lithic industries between the Late Pleistocene and Early Holocene, although not without differences across time and space (Tomasso *et al*. 2019), the focus here lies upon the potential remodelling of settlement patterns. Given the mid-latitudinal setting of the Balkans and the low productivity of the Mediterranean (Stambler 2014), cross-cultural analytical research of foraging groups, as pioneered by the late Lewis Binford (2001), suggests that Early Holocene Adriatic Mesolithic groups correspond to so-called mobile hunter-gatherers, with an expected diet mostly based on terrestrial resources, possibly supplemented by aquatic resources when available (Johnson 2014). In a similar vein, Runnels suggested a trajectory of depopulation between the Palaeolithic and Mesolithic of Greece, parallel to the loss of steppe and open forest habitats, a narrative further adapted for the Balkans by Gurova and Bonsall (2014).

The question remains whether or not these general descriptions provide a good or even reasonable match to the empirical evidence. Available data indicate a very uneven spatial distribution of the settlements (Fig. 1), with numerous inland areas almost if not entirely devoid of Mesolithic traces, with rare exceptions such as the suspected – but yet unproven – Mesolithic sites in the Požega basin, Croatia (Komšo 2006), or stratified early Mesolithic lithic artefacts from the cave site of Rastuša, Bosnia and Herzegovina, directly dated to around 9800 calBP (Jovanović *et al*. 2014). By comparison, coastal, riverine or lacustrine environments all harbour pockets of dense Mesolithic settlements. Several caves located along the eastern Adriatic coast have for instance yielded stratigraphic records of various duration for this period (e.g. Vela Spila: Dean *et al*. 2020; see also Komšo 2006), whilst Balbo and colleagues have identified several Mesolithic sites close to the

Polje Čepić, which probably corresponded to a shallow lake during the early stages of the Holocene (Balbo et al. 2009). Vander Linden and colleagues also recently uncovered the first known Mesolithic settlement long the shores of the Skadar Lake (southern Montenegro) on the site of Seočka pećina, (Vander Linden *et al*. 2015). Further north, the karstic areas of Montenegro have also yielded several Mesolithic sites, covering both the earlier and later parts of this period (e.g. Mihailović 2004, Cristiani & Borić 2016, Mercier *et al*. 2017). Last but not least, the Iron Gates, at the border between modern-day Serbia and Romania, present the highest density of Mesolithic sites in the area, with iconic locations such as Lepenski Vir or Vlasac (e.g. Borić *et al*. 2014, Bonsall and Boroneanţ 2018).

It is difficult to assess the validity of such patchy settlement evidence without considering possible biases linked, amongst other factors, to the local history of research and taphonomy. Regarding the former, the Balkans are arguably one of the less intensively surveyed parts of Europe, although it is noticeable, for instance, that several recent field operations triggered by large-scale developments such as motorways have led to the identification of numerous prehistoric sites, but hardly, if any, further Mesolithic evidence. Likewise, Gurova and Bonsall (2014) have pointed out that several well-excavated caves with extensive Pleistocene records did not yield any accompanying Holocene levels. Both examples either point to drastic behavioural changes or, indeed, to a relative depletion of the local foraging population. Conversely, the possibility of taphonomic biases, in particular in karstic environments, having destroyed – Late – Mesolithic layers should not be under-estimated (Berger and Guilaine 2009), although this hypothesis remains to be tested systematically using on-site geomorphological data. It is noteworthy for instance that, despite extensive radiocarbon dating programmes, Late Mesolithic sites especially remain elusive along vast sways of the Adriatic coast (Forenbaher *et al*. 2013), though documented in many instances across Montenegro (Cristiani and Borić 2016, Mercier *et al*. 2017), a geographical discrepancy difficult to interpret in mere taphonomic terms.

As a correlate to these few known Mesolithic sites, it is not surprising that another possible demographic proxy, summed probability distributions, suggests a low population density for the Mesolithic period (Fig. 2), either when compared with the following Neolithic or with contemporaneous trajectories in other European regions such as the Iberian peninsula (Silva and Vander Linden 2017). Admittedly, this technique remains controversial and, indeed, fluctuations in the radiocarbon record ought not to be read as directly representative of past demographic oscillations. Leaving aside the impact of the calibration curve which remains relatively straightforward to account for (e.g. Crema and Bevan 2020), the question remains as to what these fluctuations actually correspond. Naudinot and colleagues for instance have made a compelling argument for the terminal Pleistocene in northern Italy and southeastern France that changes in 14C density ought to be interpreted in light of modificationss in settlement patterns and wider landscape use (Naudinot *et al*. 2014). This being said, other strands of evidence point to a small Mesolithic population, even if areas such as the Iron Gates. Applying a Bayesian statistical framework to architectural data, Porčić and Nikolić (2016) estimate the population size of Lepenski Vir to be in the range of 15-20 individuals, with a maximum of 25-45 reached during the transition period with the Neolithic.

Ancient DNA also sheds some light on the population structure of foraging communities in the area under consideration. Extensive sampling of individuals from the Iron Gates indicates genetic proximity with the so-called Western European Hunter-Gatherer ancestry group, although these also possess several distinctive mitochondrial haplogroups (Mathieson *et al*. 2018). A possible hypothesis to account for this double pattern is that the Lepenski Vir individuals are related to a source population located in south-east Europe which would be associated with the repopulation of Europe after the Late Glacial Maximum, although this remains to be further tested (Mathieson *et al*. 2018; see also Fu *et al*. 2016). In the direct vicinity of the Balkans, it is worth mentioning the presence of a male individual buried on the early Neolithic site of Tiszaszölös-Domaháza, but whose genetic ancestry assigns to the known Mesolithic variation (Gamba *et al*. 2014). Another clue as to the possible extent of the local foraging populations is provided by a resurgence of the proportion of Mesolithic ancestry in both later Neolithic and Chalcolithic individuals across the Balkans and neighbouring regions such as Hungary, although the nature and timing of the demographic processes driving these changes in genetic admixture are far from being resolved (González-Fortes *et al*. 2017, Lipson *et al*. 2017, Mathieson *et al*. 2018).

Mobility patterns are also essential in studies of foraging groups, especially as an essential mechanism connecting otherwise small, potentially isolated communities (e.g. Kelly 1992, 2013). Strontium analysis of early and Late Mesolithic individuals in the Iron Gates area has led to the identification of a few outliers likely to be migrants, although their proportion remains very low through the course of the Mesolithic period (Borić and Price 2013). Further evidence for mobility between Mesolithic communities is also provided by exchange, as inferred by the distribution of marine and freshwater snail shells across Croatian Mesolithic sites (Komšo and Vukosavljević 2011; see also Cristiani *et al*. 2014). Lastly, claims of direct contacts between foragers from the Danube gorges and early farming communities located in northern Greece as early as 8600calBP have been made based on the identification of starch granules in dental calculus (Cristiani et al. 2016). However, the validity of this result is questionable as it is highly possible that these granules came from local wild grasses, whose presence or absence cannot be assessed in the absence of any corresponding palaeobotanical archive.

The last point to be briefly assessed concerns diet, especially as seen through the lens of stable isotopes. Obviously, this particular lens is distorted by the uneven availability of human remains, but two areas can however be highlighted. Firstly, carbon and nitrogen isotope values for coastal Mesolithic individuals from Croatia point to a mixed diet of terrestrial and marine protein (Lightfoot *et al*. 2011). This result is confirmed by zooarchaeological assemblages, for instance as in Vela Spila with indication of – possibly seasonal - fishing of chub mackerel in the early

Mesolithic, and a wider range of coastal species in later phases (Rainsford *et al*. 2014). Secondly, both zooarchaeological and stable isotope data for the Danube gorges indicate a high reliance upon fish intake during the entire early Holocene sequence, showing how foraging populations took full advantage of the local ecosystem (Bonsall *et al*. 2015).

Neolithic farmers and herders

During the first half of the 9th mill calBP, the first cultigens and animal domesticates appear in continental Europe, having been identified at sites in both northern and southern Greece (e.g. Franchthi: Perlès *et al*. 2013; Dikili Tash: Lespez *et al*. 2013; Mavropigi: Karamitrou-Mentessidi *et al*. 2015). This set of new species is without doubt introduced from western Anatolia after dispersal from the original centres where the process of domestication had been initiated nearly two millennia before (e.g. Zeder 2011). It is important to recognise that, although the new domesticates and elements of associated material culture are often referred to as a "Neolithic package", there appears to be extensive geographical and temporal variation in the variety and proportion of the various components of this package (e.g. Arbuckle *et al*. 2014 for the initial dispersal across modern-day Turkey; see also Perlès 2001, Çilingiroğlu 2005), a situation well-documented for the Balkans. This section thus reviews empirical evidence for variation in Neolithic agricultural systems, focusing on potential factors responsible for shaping this variation, especially in environmental and ecological terms.

After their initial distribution across Greece and southern Bulgaria during the first centuries of the 9th mill calBP, domesticated plants and animals experience a further episode of dispersal towards the end of the same millennium. This second dispersal event concerns both the Danube and Adriatic basins, under markedly different archaeological and spatio-temporal configurations (e.g. Bocquet-Appel *et al*. 2009). Across the Danube basin, this spread corresponds to the Starčevo-Körös-Criş complex and is characterised by a fast expansion pace, translating into a Neolithic presence reaching the Pannonian basin by c. 8000 calBP. The advance of the Neolithic corresponds to the Impressa complex In the Adriatic basin, and is comparatively much slower as farming only reaches its northern end around 7700-7600 calBP (Fig. 3).

As previously mentioned, this complex spatio-temporal patterning is paralleled by variation in agricultural practices, possibly as the new farming communities encounter new environmental conditions. Such process of adaptation is for instance evident in the general new preference for cattle associated with Early Neolithic sites in Bulgarian Thrace, and can be explained by the availability of more favourable grassland when compared to the conditions from the Near East (Conolly *et al*. 2012). Likewise, several researchers have stressed that the initial Neolithic settlement pattern, as documented by Greek and Bulgarian sites, favours specific, spatially-restricted ecological niches characterised by mild climatic conditions and productive soil types (e.g. Struma river valley: Krauß *et al*. 2018, Whitford 2019). Krauß and colleagues in particular have argued that this choice was dictated by the conditions linked with the 8.2kcal BP event, a challenging period of climatic instability, including potential harsh winters and increased seasonality (Krauß *et al*. 2018; see also Weninger *et al*. 2014). Likewise, Ivanova and collaborators have shown that this environmental pressure explained some of the variation in local early Neolithic farming systems, though this signal remains small and mostly limited to zooarchaeological rather than archaeobotanical data (Ivanova et al. 2018).

Such close reliance upon specific ecological niches for the duration of the 8.2 calBP event implies that these conditions possibly hindered further dispersal of the Neolithic economy. Indeed, the end of this event coincides with the dramatic resurgence of the dispersal previously described (e.g. Bocquet-Appel *et al*. 2012 for a quantitative appraisal of this question). This apparent correlation is suggestive indeed but, in order to turn it into a causal relationship, more data are required to characterise the exact local environmental footprint of the 8.2calBP event and the immediately following centuries. For instance, at the continental scale, Europe can be divided in three climatic bands during the 8.2calBP event, with a southernmost one associated with high seasonal contrast and encompassing Greece and the southern Balkans, and immediately north of it a fresh and humid area (Magny et al. 2003; see also Berger and Guilaine 2009). Regardless of the precise location of the demarcation between these two general units, it remains unclear how and to what extent the new climatic conditions would affect them and effectively translate into either more favourable ("pull" factors) or harsher ("push" factors) environments for Neolithic farmers.

This being said, the renewed expansion of early farming across the Danube catchment crossed over an array of biogeographical regions (pannonian, continental, and alpine, using modern-day classes as closest available analogues), thus pointing to an apparent relaxation of the constraints (self-)imposed upon these communities. This diversity is particularly mirrored in zooarchaeological assemblages, although the adaptive dimension of this process is not straightforward. Sites in the Iron Gates area for instance present a high proportion of cattle. By contrast, sites in the Pannonian plain are dominated by a caprine-based economy, a trend lasting until c. 7700calBP and possibly reflecting preferred options from the original source of the local Neolithic, as can also be observed for instance in Macedonia (Orton *et al*. 2016). Analysis of the mortality profiles for both sheep and goats suggests husbandry management techniques linked to dairying and meat acquisition, with possible site-driven preferences (Gillis *et al*. 2019). In all areas, hunting constitutes a limited activity (Orton *et al*. 2016). Overall, this variation is such that zooarchaeological assemblages from the Danube catchment present overall less coherence than data drawn from the Adriatic basin (Gaastra et al. 2019). Variation in archaeobotanical assemblages is less discernable though still occasionally documented, for instance barley being rare in Serbia but dominant in Hungary (de Vareilles 2018).

The farming expansion across the Adriatic basin is likely to have largely proceeded via boats, as indicated by a settlement pattern strongly biased towards the coastlines in the earliest stages of the Neolithic, with the use of inland corridors documented in few instances (e.g. karstic Montenegro:

Borić *et al*. 2019). This being said, a generalised use of the Adriatic hinterland seems a comparatively later phenomenon (e.g. Vander Linden et al. 2014). It is also noticeable that, despite its likely reliance upon maritime travel, the progression of the Neolithic front across the Adriatic is comparatively slower, only reaching the shores of the Pô valley a few centuries later than early dates for the southern Adriatic, although at that point in time the Neolithic way of life has progressed at breakneck speed across the Tyrrhenian Sea and the rest of the Western Mediterranean basin (e.g. Binder *et al*. 2017). This dispersal and the concomitant archaeological variation occur within a relatively homogeneous biogeographical setting, with a SE-NW gradient towards less dry climates and accordingly slightly different landscapes. As for the Danube basin, the impact of this ecological factor is mostly noticeable in early Neolithic zooarchaeological assemblages (Gaastra and Vander Linden 2018). Sites located on the eastern Adriatic and southern Italian coast are dominated by sheep and goats, constituting 50 to over 90% of the bone assemblages. Statistical modelling of tooth eruption data indicates that, as for the Danube basin, husbandry techniques were driven by the acquisition of both meat and dairying products (Gillis *et al*. 2019), the latter in agreement with the results of residue analysis from pottery and meat (Debono Spiteri *et al.* 2016; McClure *et al*. 2018). Further north, pigs and, to a lesser extent, hunting remain marginal, but the proportion of cattle breeding increases parallel to the growing availability of pasture lands under wetter pluviometric regimes. The importance of this last pattern must however be minimised: whilst it indicates that early farmers adapted their behaviour to local conditions, this should not lead to any deterministic vision as, during later Neolithic periods with noticeably drier climate, this prevalence for cattle remains dominant in several areas (Gaastra and Vander Linden 2018). Variation within Adriatic archaeobotanical assemblages is limited, although there are some obvious differences with the Danube counterparts, such as the low occurrence of peas, perhaps related to the fact that this species is less tolerant to drought (de Vareilles *et al.* 2020). This latter trait is also a facet of a wider process of drop in crop diversity when compared to archaeobotanical assemblages for the Eastern Mediterranean (Colledge *et al*. 2005).

Human remains are scarce, but less so than for the Mesolithic, and stable isotope analysis thus provides a good regional insight into Neolithic diets. Data for inland Croatian Neolithic indicate reliance over terrestrial resources, whilst there is more variation for the Coastal Neolithic, pointing to a diet of terrestrial resources supplemented by marine sources (Lightfoot *et al*. 2011). This last pattern is broadly comparable to the picture gained for the Mesolithic-Neolithic transition period in the Iron Gates, also showing a mix of terrestrial and aquatic resources, the latter becoming less important through time (Bonsall *et al*. 2004).

Demography and mobility

The field of Neolithic studies has been dominated by a decades-long argument on whether incoming communities were responsible for the introduction of farming or foragers were rather transmitting amongst themselves the new skill set. Whilst pretty much every single component of the archaeological record has been used by proponents of either position to support their respective views, the advent of ancient DNA and, to a lesser extent, of SPDs on the scene has dramatically changed the picture so that archaeologists are now able us to reconsider population and dispersal dynamics.

Of the two aforementioned techniques, aDNA has arguably the highest profile and provides in many respects the strongest evidence for identifying a new, exogenous population. Regardless of the controversies related to the difficult marriage between aDNA and archaeology (e.g. Johanssen *et al*. 2017, Racimo *et al*. 2020), analysis of numerous early Neolithic samples from the Danube catchment and neighbouring areas demonstrates without doubt that the Early Neolithic period indeed corresponds to the introduction of a new genomic component in the European genetic variation (e.g. Mathieson *et al*. 2018). Without much surprise perhaps, the geographical origins of this genomic component can be traced back to the Levant, that is the same area where plant and animal domesticates originate from (Lazaridis *et al*. 2016). This coincidence thus provides undeniable evidence that the new farming economy was introduced by a new population. However, the debate is far from being settled as the scale and exact mechanisms of this dispersal remain difficult to assess on sole genetic grounds. The genetic signal is very strong as the majority of early Neolithic individuals, but for a very few exceptions such as the already mentioned individual from Hungary (Gamba *et al*. 2014), present very low levels of genetic admixture with the preceding local foragers. However, as already said, later Neolithic and Chalcolithic samples see a resurgence of the Mesolithic-related ancestry, possibly suggesting further mixing between Neolithic and Mesolithic groups than suggested by early Neolithic samples alone (González-Fortes *et al*. 2017, Mathieson *et al*. 2018). Although no samples are available at the time of writing for the Adriatic basin, results from the rest of the Mediterranean Sea tell a similar story of new incoming population from the Levant associated with the onset of plant and animal domesticates (e.g. Lipson *et al*. 2017). It is worth pointing out however that inferred dates for Mesolithic-Neolithic genetic admixture identified in early Cardial individuals suggest that the corresponding low proportion of Mesolithic ancestry was acquired earlier during the dispersal across the Mediterranean, without further precision as to where and when exactly (Lipson *et al*. 2017).

The second technique providing us with a new opening onto past demography is SPDs. Keeping in mind the previously discussed difficulties in reading SPDs solely in demographic terms, in the present case, several arguments point to a strong demographic signal associated with the onset of the Neolithic across both Adriatic and Danube basins (see Silva and Vander Linden 2017, Vander Linden and Silva 2021 for full discussions). Firstly, a sharp change in the SPDs contemporaneous with the timing of the introduction of farming can be identified in all regions (see also Porčić *et al*. 2016, 2020 for Serbia; Fig. 2). Secondly, this change in SPDs is incompatible with a predictive model based on sole growth from the known density for the previous Mesolithic (Silva and Vander Linden 2017). Thirdly, by contrast a best fit between empirical data and a theoretical population model is achieved when using a logistic growth curve, whereby the population under study experiences a sharp change in its growth until reaching a maximum threshold, generally considered to be dependent upon the carrying capacity of the local environment (Vander Linden and Silva 2021). The first and second of these points suggest that the demographic trajectory of the sole local foraging Mesolithic population is incompatible with the empirical evidence and thus, concur with the ancient DNA data to identify the existence of an early Neolithic migratory event. The third point indicates that, in addition to the introduction of this new population, contemporary demographic regimes experience a dramatic shift, characterised with sustained higher growth rate over several generations, a signature compatible with the expected demographic properties favoured by the new farming economy (so-called “Neolithic Demographic Transition”: Bocquet-Appel 2011, Bocquet-Appel & Bar-Yosef 2008).

If the general impression is thus one of large-scale dispersal associated with the early Neolithic, the question remains if this pattern can be identified at site-level (that is outside the remits of ancient DNA sampling obviously), and to what human mobility constituted an integral component of the lives of these farming communities. Given its impressive record of human remains spanning the Mesolithic and Neolithic sequences, it is unsurprising that the Iron Gates constitute the key area for which data are available. There appears to be extensive variation in ^{87}Sr/S^{86}Sr values amongst Mesolithic-Neolithic transition and Early/Middle Neolithic individuals, translating into more outliers, i.e. “non-locals” or “migrants”, being identified, in particular on the site of Lepenski Vir, as well as the nearby site of Ajmana, located in a different part of the local landscape, more suitable for agriculture (Borić and Price 2013). Most of these “non-locals” are women, suggesting post-marital residency rules and a wider network linking the old Mesolithic enclave to newly founded Neolithic settlements located in its immediate vicinity. Noticeably, a comparable situation has been observed in Hungary for the Starčevo period on the site of Alsónyék-Bátaszék (Depaermentier *et al*.

2020). However, one should not make hastily generalisation as, by contrast, low human mobility is recorded at the Greek early Neolithic sites of Revenia and Neo Nikomedia (Whelton *et al*. 2018) Further material evidence indicates that early Neolithic communities across the Balkans were closely inter-linked together. For instance, so-called Balkan flint, most likely sourced from Bulgaria (Gurova and Bonsall 2014b), is in wide circulation across the entire Balkan peninsula and occurs in varied quantities across numerous Starčevo sites (Jovanović and Vander Linden 2019). Likewise, obsidian is also imported, though in much lower number and tends be rare, if not entirely lacking from most Starčevo sites (e.g. Jovanović and Vander Linden 2019). The situation along the eastern Adriatic coast is particularly interesting. There, Early Neolithic lithic assemblages are indeed dominated, not by locally available raw materials, but by Gargano chert mined in and imported from the eponymous site in Foggia, Italy (Forenbaher and Perhoč 2017). Forenbaher and Perhoč (2017) interpret this pattern as, for the earlier stages of the Neolithic, an expression of newly arrived communities relying upon existing trade routes rather than scouting for locally available materials, and, for later periods, continuous import of high-quality cross-Adriatic products (as traces of in situ débitage remain rare in Croatian Adriatic sites).

Conclusion

Keeping in mind that new Mesolithic – and Neolithic as well – sites are by definition bound to be found in the future, the entire range of available evidence is in agreement with the theoretical biogeographic-based expectations of a depleted local Mesolithic meta-population, composed of small communities relying mostly upon terrestrial and, when available, marine/riverine resources. This statement should not be confused for a mere deterministic argument, but rather implies that the undeniable existing variation occurred within a framework shaped by the new Holocene environments, to which late foraging communities were adapted. Likewise, as the new incoming Neolithic communities progressed, they encountered changing climates, environments and landscapes, which influenced their behaviour to varying degrees. The impact of the 8.2calBP event remains debatable: the prevalence of earliest Neolithic settlements in specific river valleys, less subject to the contemporaneous Rapid Climatic Change conditions, is well-established, but the coincidence between the resuming expansion of farming and the end of the 8.2calBP event is suggestive, though remains to be further tested.

This secondary dispersal of plant and animal domesticates and associated human populations occurred in two broadly different ecological corridors, each with their own specific characteristics and associated archaeological variation. The preference for cattle observed in various areas rich in grasslands is a likely example of the migratory farmers adapting to their new settings. Yet, the earlier horizon of high proportion of sheep and goats in the Pannonian basin acts as a cautionary tale against any narrative dominated by the influence of environmental factors. Likewise, the somewhat limited ecological pressure on crops points to the existence of other forces at play, possibly cultural, in shaping variation. This being said, the exact nature of these forces largely remains to be explored. For instance, it has been suggested elsewhere, on the basis of the results of an agent-based model, that a relative drop in diversity in assemblages, as seen across the Mediterranean Sea and central Europe (Colledge *et al*. 2005, de Vareilles *et al*. 2020), parallel to the advance of the Neolithic front could be explained as the outcome of a series of founder-effects, whereby only parts of the initial options available (e.g. crops, technologies) are taken by the migrating subset of populations (Drost and Vander Linden 2018) .

Humans and environments thus share an intricate and complex history in the Balkans during the early part of the Holocene. It is noticeable that, at the difference of later periods marked by extensive anthropogenic impacts upon the landscapes by humans (Marquer *et al*. 2017), this is a tale, not of mere determinism, but one of ecological frameworks and human practices enfolding within them, with all the variation this allows for.

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Figure 1: distribution map of ^{14}C-dated Mesolithic sites in the research area

Figure 2: summed probability distributions of 14C dates for the Mesolthic and Neolithic periods in the research area, using a binning of 100 years. The dotted line corresponds to a 200 years rolling means

Figure 3: distribution map of ^{14}C-dated Neolithic sites in the research area

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